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Preserved Ammonitellas of *Scaphites* (Ammonoidea, Ancyloceratina)

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ABSTRACT

Ammonitellas, embryonic shells of ammonites, occur in the Upper Cretaceous (Turonian) of Colorado associated with adults of *Scaphites ferrensis* Cobban. They average 650 μm in diameter and are similar to the embryonic whorls of the associated scaphite species to which they probably belong. They terminate at the primary constriction and accompanying varix but display variation in number of embryonic septa from shells with only a single prismatic prosepium and body chamber angles of 290° to shells completely filled with septa

and body chamber angles less than 60°. However, the lack of a body chamber during life is an impossibility and suggests that the primary varix must be a point of weakness for postmortem breakage. This, plus the presence of young postembryonic shells that extend *beyond* the primary constriction and reveal two to six septa, implies that variation in number of embryonic septa above the prosepium may be false. Based on functional morphology, the newly hatched ammonite may have led a planktic existence for some time after hatching.

INTRODUCTION

Embryonic shells of ammonites (called ammonitellas by Drushits and Khiami, 1970) have been discovered in Mesozoic deposits throughout the world (Dreyfuss, 1933; Trueman, 1940; Wetzel, 1959; Drushits and Khiami, 1970; Birkelund, 1979; Blind, 1979; Kulicki, 1979; Bandel, 1982; Dietl in letter cited in Bandel, 1982; Landman, 1982a). Inspection of intact, well-preserved shells permits the determination of the number of embryonic septa and the patterns of embryonic development. The mode of life of these newly hatched ammonites is based on their functional morphology, faunal association, and mode of occurrence. These observations on morphology and mode of life form the basis for comparison with the early ontogenies of

other shelled cephalopods. I report here the results of a study on minute ammonite shells identified as ammonitellas of *Scaphites* from the Upper Cretaceous (Turonian) of Colorado.

MATERIAL AND METHODS

Several thousand minute ammonite shells were discovered in the body chambers and adhering matrix of 15 mature specimens of *Scaphites ferrensis* Cobban, an Upper Cretaceous (Turonian) heteromorph. These 15 specimens were collected by W. A. Cobban in 1967 from the top of the Juana Lopez Member of the Mancos Shale 1.7 miles northeast of Austin in Delta Co., Colorado

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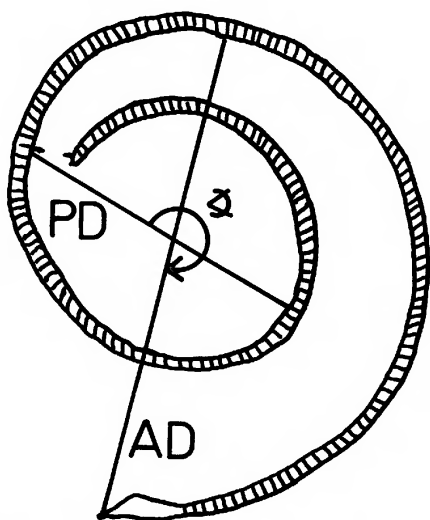


FIG. 1. Diagram of median section of ammonitella illustrating protoconch diameter (PD), ammonitella diameter (AD), and ammonitella angle (α). The ammonitella angle is equivalent to the body chamber angle of an ammonitella with only a prosepium.

(USGS Locality no. D6022). No other ammonite species were present at this locality (Cobban, personal commun., 1984). The body chambers of these 15 specimens are largely internal molds and are composed of calcareous shale and coarsely crystalline calcite in addition to the accumulations of small ammonites. These ammonites, less than 1 mm in diameter, co-occur with numerous slightly larger specimens up to 2 mm in diameter.

The original shell microstructure is generally preserved and the chambers are filled with shale and orange-colored calcite. Associated with these ammonites are thousands of tiny clams, fish scales, and vertebrae. The clams range from 300 to 550 μm in length and appear to have already undergone metamorphosis from a planktic larval state (Lutz, personal commun., 1984).

Several minute ammonite specimens were worked out of the matrix but tended to break or emerge as internal molds without shell. A more reliable method to view the entire specimen and avoid breakage was to embed shells still retaining matrix in epoxy. Prior to embedding, these specimens were mounted onto an epoxy base and oriented. They were subsequently ground and polished to the median plane of symmetry through the siphuncle. All size measurements and counting of septa were made on the median plane. Specimens were also uncovered by grinding down chunks of ammonitiferous material. This method sometimes revealed the most complete specimens but because orientation was not preset, measurements of diameter and other dimensions were subject to error. Although preservation was generally very good, the presence of calcite fracture surfaces and obscuring sedimentary matrix in some shells made counting of septa problematic, so such shells were omitted from study. Therefore, of 85 polished sections prepared, 65 were used in this study.

Five standard measurements were made

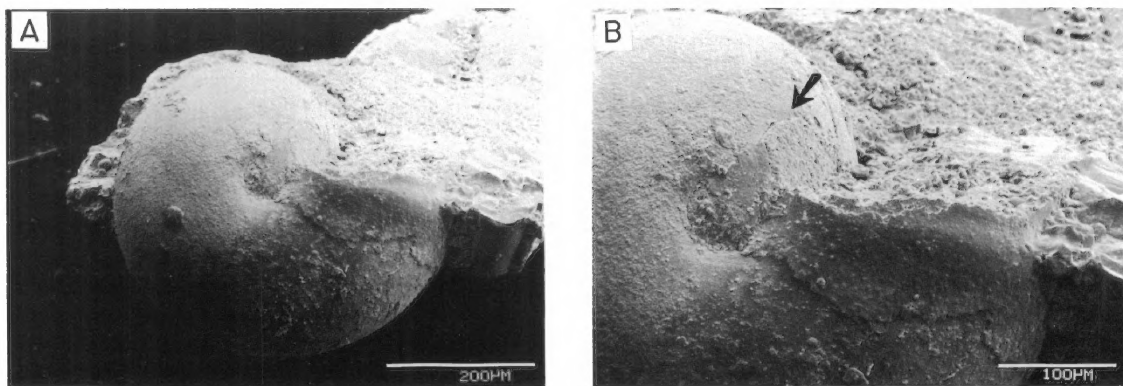


FIG. 2. (A). Ammonitella of *Scaphites* freed from the matrix. It is a steinkern but retains some shell near the primary constriction which displays a tuberculate micro-ornamentation (B). The arrow points to the ventral saddle of the prosuture, the only suture present on the specimen.

TABLE 1

Ammonitella Diameter (in Microns), Angle (in Degrees), and Protoconch Diameter (in Microns) for Minute Ammonite Shells from USGS Locality No. D6022^a

	Group I			Group II			Group III			Group IV			<i>Scaphites ferronensis</i> and <i>Scaphites whitfieldi</i>		
	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n
AD	645.7	77.76	18	605.8	33.05	19	617.3	39.42	10	648.0	67.1	15	619.0	42.49	199
AA	286.6	11.66	16	283.8	18.23	18	280.44	6.00	9	286.9	11.26	14	284.0	11.68	169
PD	322.3	21.30	9	327.1	10.86	9	319.1	15.79	7	331.0	19.31	3	320.1	29.09	184

^a Group I refers to shells that end in the primary varix and possess only a prosepium. Group II refers to shells that end in the primary varix and are completely filled with septa. Group III refers to shells that end in the primary varix and possess 2 to 8 septa. Group IV refers to shells that extend beyond the primary varix. The last column on the right represents values for adults of *S. ferronensis* and *S. whitfieldi* from Landman, 1982b.

Abbreviations: AD, ammonitella diameter; AA, ammonitella angle; PD, protoconch diameter; \bar{x} , mean; SD, standard deviation; n, number of specimens measured.

on all specimens wherever possible (fig. 1). (1) Protoconch diameter taken through the center of the protoconch and the ventral edge of the prosepium. (2) Maximum diameter of the ammonitella measured through the center of the protoconch and the primary varix, the conspicuous nacreous thickening near the end of the first whorl (Landman and Waage, 1982). (3) Ammonitella angle measured from the prosepium to the end of the primary constriction and accompanying varix. This is equivalent to the body chamber angle of an ammonitella with only a prosepium. (4) Body chamber angle. This measurement may be particularly liable to underestimation because postmortem breakage may have shortened the body chamber. (5) Number of septa counting the prosepium as one septum.

RESULTS

Fifty shells in polished section terminated at the end of the primary constriction and accompanying varix or at the varix trace. These features mark the end of the embryonic shell or ammonitella (Drushits and Khiami, 1970; Drushits, Doguzhayeva, and Mikhaylova, 1977; Kulicki, 1979; Tanabe, Fukada, and Obata, 1980; Bandel, 1982; Landman, 1982a). Similar shells freed from the matrix and viewed in the round displayed the tuberculate micro-ornamentation previously observed on the embryonic whorls of various species of *Scaphites* (fig. 2; Bandel, Landman,

and Waage, 1982). In exceptionally well-preserved specimens, the prosepium appeared prismatic; all later septa appeared nacreous. The caecum and prosiphon were not preserved in any specimens.

Based on the number of septa present these 50 ammonitellas fell into three groups (fig. 3A–C, table 1).

I: Twenty specimens featured only the prosepium with body chamber angles (equivalent to ammonitella angles) ranging from about 270° to about 310° (average approximately 290°, fig. 4). Their average diameter was about 650 μm . Their protoconch diameter averaged about 320 μm .

II: A nearly equal number (19) were completely filled with septa, with body chamber angles less than 60°. In most specimens, the primary varix was perfectly intact and marked the end of the shell. In a few specimens the varix was broken. Broken, curved fragments of shell were sometimes observed near the specimens. The ammonitella diameter and angle of these specimens averaged about 610 μm and 280°, respectively. Their protoconch diameter averaged about 330 μm .

III: Eleven specimens featured two to eight septa. Shells with two septa had body chamber angles of 250° to 260°. Shells with four septa had body chamber angles of 200° to 210°. Those with six to eight septa had body chamber angles less than 150°. Ammonitella diameter and angle averaged about 620 μm and 280°, respectively. Protoconch diameter

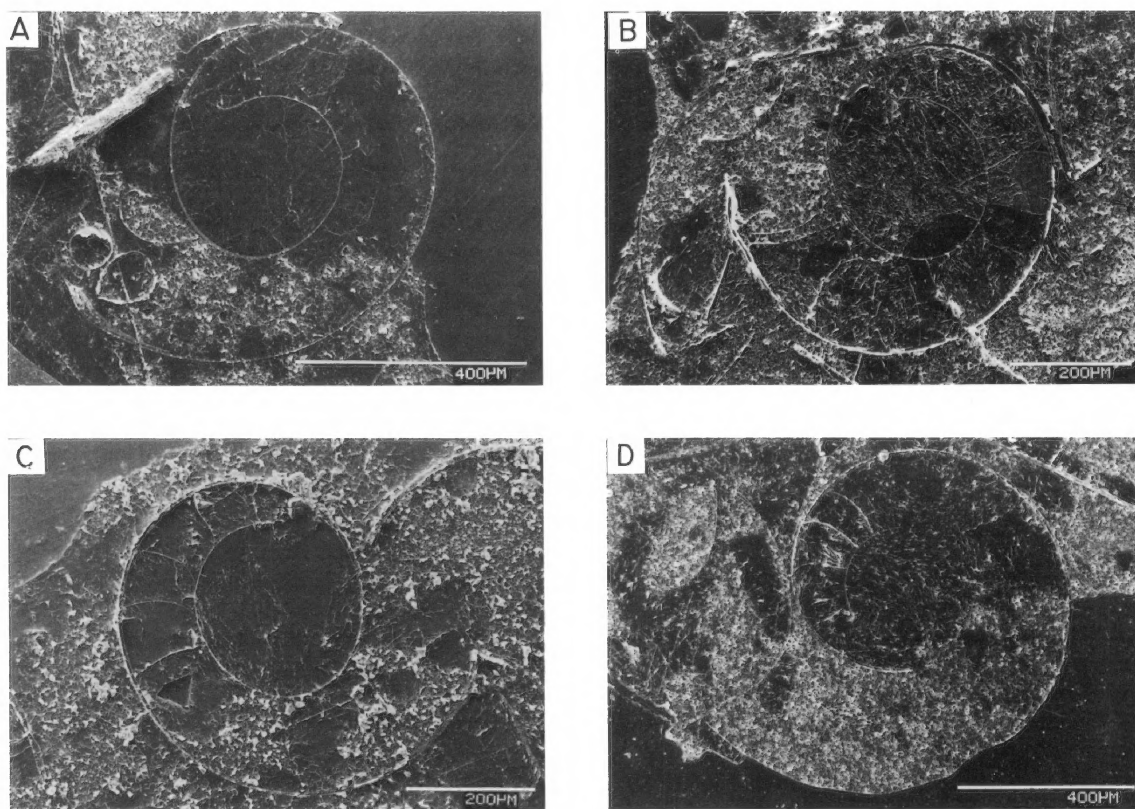


FIG. 3. Median cross-sections of minute ammonite shells from the Upper Cretaceous (Turonian) of Colorado. Shells A–C terminate in the primary constriction and accompanying varix, features that mark the end of embryonic development. Shell A displays only a single prosepium, Shell B is filled with septa (the “color changes” between adjacent chambers help to emphasize the positions of the septa), and Shell C displays 6 septa. Shell D extends beyond the varix trace (the impression of the primary varix on the steinkern) and is clearly postembryonic. It possesses six septa.

averaged about $320\ \mu\text{m}$. The termination in the primary varix was frequently clear-cut but sometimes indefinite.

Another 15 specimens in polished section were slightly larger, measuring up to 2 mm in diameter. These shells extended beyond the primary constriction with intact or broken body chambers. Their ammonitella diameter and angle averaged about $650\ \mu\text{m}$ and 290° , respectively. Their protoconch diameter averaged about $330\ \mu\text{m}$ (fig. 3D, table 1). Similar shells freed from the matrix and viewed in the round displayed the same tuberculate micro-ornamentation on their embryonic whorls as previously observed on the smaller shells and on the embryonic whorls of *Scaphites*. The shape of the early postem-

bryonic whorls also resembled the shape of the corresponding whorls of closely related species of *Scaphites* (fig. 5). Three of the 15 shells featured two, six, and six septa with body chambers extending beyond the primary constriction. Their body chamber angles measured 270° , 220° , and 280° , respectively.

In all the specimens measured, the protoconch diameter was approximately half the ammonitella diameter and the two measurements showed a positive correlation. The correlation coefficient equaled 0.707 (fig. 6).

DISCUSSION

ATtribution to *Scaphites*: All the specimens studied including the postembryonic

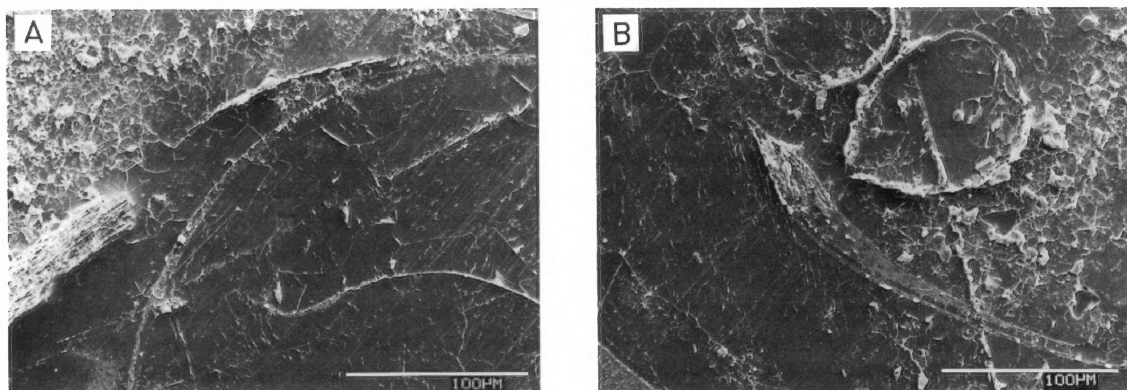


FIG. 4. Close-up of prosepium (A) and primary varix (B) of specimen shown in figure 3A.

shells show considerable overlap in protoconch diameter, ammonitella diameter, and ammonitella angle (fig. 7, table 1). The averages are similar and extreme values are probably artifacts due to measurement of poorly oriented shells. These values are similar to those obtained for the embryonic whorls of adults of co-occurring *S. ferronensis* and of the closely related species *S. whitfieldi* Cobban. In a survey of nearly 200 adults of these two species, the protoconch diameter, ammonitella diameter, and ammonitella angle averaged 320 μm , 620 μm , and 280°, respectively (table 1; Landman, 1982b). The embryonic shells and the embryonic whorls of the young postembryonic shells also display the same tuberculate micro-ornamentation as that present on the embryonic whorls

of *Scaphites*. They also display the same sequence of septal microstructure; the prosepium is prismatic and all later septa are nacreous. Additionally, the shape of the whorls of young postembryonic shells resembles the shape of the corresponding whorls of *S. ferronensis* and *S. whitfieldi* (fig. 5). The body chamber angles of intact postembryonic shells measure 220° to 280° and are similar to values obtained for a sample of 40 juveniles of the Coniacian and Santonian scaphite species *S. preventricosus* Cobban and *Clioscaphites vermiformis* (Meek & Hayden), respectively (Landman, 1982b). Finally, *S. ferronensis* is the only ammonite present at this locality, and in view of the above similarities the minute ammonite shells are referred to the genus *Scaphites*.

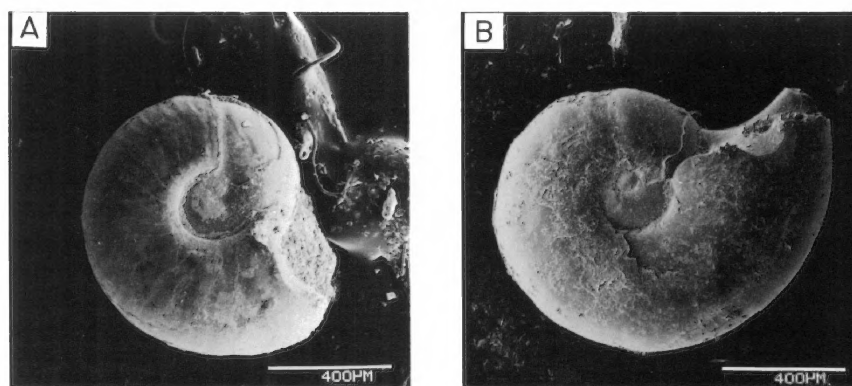


FIG. 5. Comparison between a postembryonic specimen associated with the ammonitellas (A) and the early whorls of an adult *S. whitfieldi* (B). The primary constriction (or varix trace) is on top.

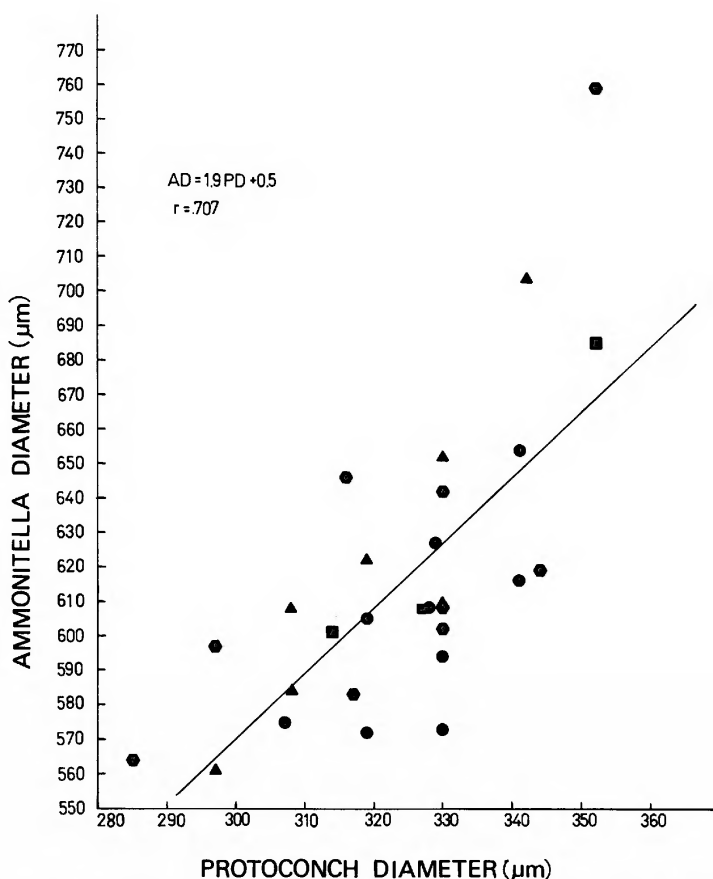


FIG. 6. Graph of protoconch diameter versus ammonitella diameter for minute ammonite shells from USGS Locality no. D6022. ● refers to shells that end in the primary varix and possess only a prosepium. ● refers to shells that end in the primary varix and are completely filled with septa. ▲ refers to shells which end in the primary varix and possess two to eight septa. ■ refers to shells that extend beyond the primary varix.

EXACT NATURE OF EMBRYONIC SHELL: The primary constriction and accompanying varix mark the end of the embryonic shell. Of the 50 minute shells that end in the primary varix, 20 possessed only a prismatic prosepium (fig. 3A). Their body chamber angles average 290° and approach the body chamber angles of older scaphite juveniles (Landman, 1982b). The presence of only a prismatic prosepium within the embryonic shell agrees with claims that the transition from prismatic to nacreous septa coincides with the boundary from embryonic to postembryonic development (Drushits, Doguzhayeva, and Mikhaylova, 1977; Birkelund and Hansen, 1974). Nacreous septa only appear in the postem-

bryonic stage and this pattern of septal occurrence has actually been documented in preserved ammonitellas of *Quenstedtoceras* and *Baculites* (Blind, 1979; Landman, 1982a).

The 20 shells of *Scaphites* sp. are, however, accompanied by 11 other ammonitellas which possess two to eight septa, one to seven of which are nacreous (fig. 3C). These 11 shells terminate in the primary varix although this feature is sometimes broken. Their body chamber angles are up to half that of the shells with only a prosepium. A comparison of average ammonitella diameter and angle between the two groups, however, indicates no significant difference that could suggest a correlation between number of septa and di-

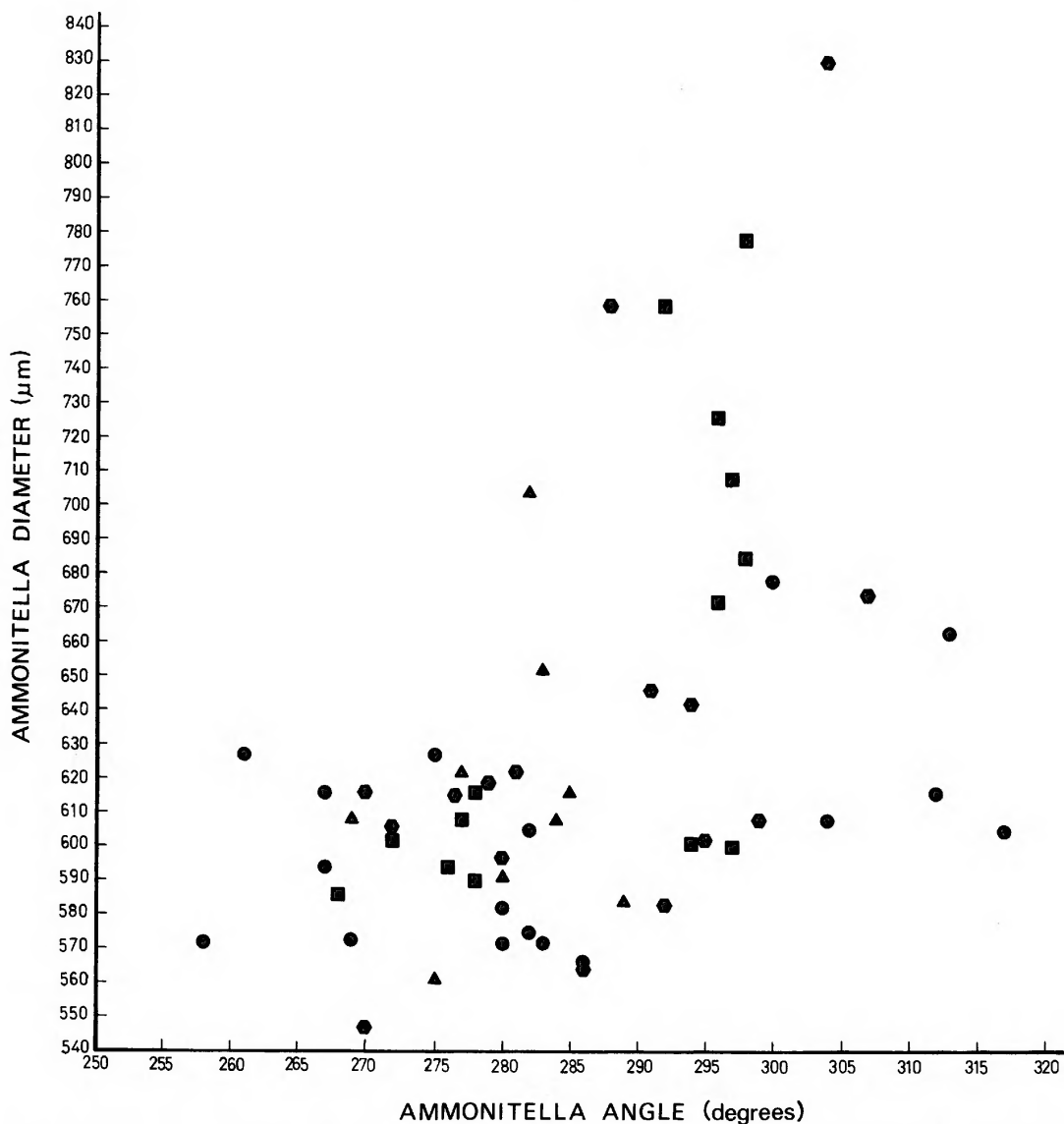


FIG. 7. Graph of ammonitella angle versus ammonitella diameter for minute ammonite shells from USGS Locality no. D6022. Symbols are the same as in figure 6.

ameter or number of septa and ammonitella angle. Do these 11 shells express the range of variation in number of embryonic septa possible within a genus? This would also imply that nacreous septa may be deposited embryonically. Such species-specific variation in the number of embryonic septa has, in fact, been demonstrated in modern sepioids (Bandel and Boletzky, 1979).

However, two lines of evidence suggest

caution in interpreting this variation in number of embryonic septa as natural. First, an additional 19 shells end in the primary varix and are nearly or completely filled with septa (fig. 3B). Their termination at the end of the primary varix is often quite precise although sometimes this feature is broken and stray fragments of shell are located nearby. The lack of a body chamber during life is impossible and implies that additional postem-

bryonic shell must have existed. The primary varices of the shells with two to eight septa are similarly complete although breakage at their anterior end is also sometimes indicated. As pointed out by Kulicki (1974, 1979), the primary varix strengthens the apertural edge of the ammonitella and abuts against the new postembryonic outer shell. This junction provides a natural point for postmortem breakage and separation of embryonic from postembryonic shell.

Secondly, three postembryonic shells with two to six septa have preserved body chambers extending beyond the primary constriction and accompanying varix (fig. 3D). Their body chamber angles range from 220° to 280° although even these values may be underestimates due to postmortem breakage. Two of the specimens, with six septa, display larger body chamber angles than shells with the same number of septa that end in the primary varix. The body chamber angles of these two postembryonic shells are also nearer the body chamber angles of larger juveniles of *Scaphites* (Landman, 1982b).

These facts plus the abundance of shells with a single prismatic proseptum suggest that the shells with two to eight septa ending in the primary varix do not represent natural variation in number of embryonic septa but are postmortem artifacts. A similar interpretation may apply to data derived from finds of preserved ammonitellas of *Baculites*. Upper Cretaceous (Coniacian–Santonian) ammonitellas of *Baculites* from Montana ending in the primary varix revealed only a prismatic proseptum with body chamber angles of approximately 330° (Landman, 1982a). Young postembryonic specimens with outer shells extending beyond the primary constriction and forming a shaft displayed nacreous septa. A broken embryonic shell of *B. chicoensis* (Trask) from the Campanian of California also revealed only a prismatic proseptum (Smith, 1901). However, complete ammonitellas of *Baculites* from the Campanian of Jordan showed five to seven septa with body chamber angles of approximately 180° , almost half that of the North American species (Bandel, 1982). Although these Jordanian shells were silicified and septal microstructure could not be verified, based on the North American species, some of the sep-

ta were probably nacreous. Such variation in the number of embryonic septa in the same genus over broad geographic areas cannot, of course, be ruled out, but the results of the present study strongly suggest that such variation is the result of postmortem breakage.

MODE OF LIFE AT HATCHING

FUNCTIONAL MORPHOLOGY: The embryonic shells average $650\ \mu\text{m}$ in diameter and represent the lower end of the size spectrum of ammonite embryonic shells. The embryonic shells of Mesozoic ammonites range from approximately 600 to $1500\ \mu\text{m}$ in diameter (Zakharov, 1972) and are small relative to adult body size, e.g., approximately 2 percent of the adult body size of *S. ferrensis*. All embryonic shells consist of a body chamber, a protoconch, and one or possibly more septa. A caecum and prosiphon are also reported in the preserved embryonic shells from Ul'Yanovsk (Drushits and Khiami, 1970) although these features are not preserved in the ammonitellas studied here. The protoconch or initial chamber is relatively large and its diameter is approximately one-half that of the ammonitella. Protoconch diameter is also positively correlated with ammonitella diameter both within and among species (fig. 6; Tanabe, 1979; Landman, 1982b).

Based on the appearance of the embryonic ammonite shell, at least two modes of life have been suggested. Wetzel (1959) envisioned that the fragile shells of newly hatched ammonites would allow them to crawl along the bottom and only after secretion of several more whorls would they become free swimming. He argued that the caecum, at least initially, would perform a function other than that related to buoyancy regulation. On the other hand, Kulicki (1974, 1979), Birkelund and Hansen (1974), Drushits, Doguzhayeva, and Mikhaylova (1977), and Landman (1982a, 1982b) have proposed that the newly hatched ammonite was planktic. A planktic mode of life at hatching is common among many modern coleoids including planktic and nektic squids, sepioids, and benthic octopods with relatively small eggs (Boletzky, 1974, 1977).

At a diameter of approximately 1 mm, the newly hatched ammonite would belong to the

macroplankton and would approach the size of the largest modern bivalve and gastropod planktic larvae (Ockelmann, 1965; Spight, 1976). The potentially buoyant protoconch, comprising a large portion of the ammonitella, would act as a float. The caecum and possibly the prosiphon would function as part of the buoyancy system. Nevertheless, some time would have had to elapse before or after hatching to allow the evacuation of liquid from the protoconch (Mapes, personal commun., 1984). After hatching, the ammonite could have remained in the plankton for several days or weeks depending on the size of the embryonic shell and the mode of life of the adult. During this time, it may have been passive (Birkelund and Hansen, 1974) or dependent on vertical movements (Kulicki, 1974). However, the presence of a ventral sinus in the growth lines immediately after the primary constriction may indicate the existence of a hyponome which could have permitted more active swimming (House, 1965; Erben, Flajs, and Siehl, 1969).

FAUNAL ASSOCIATION AND OCCURRENCE: The embryonic shells studied occur profusely in the body chambers and adhering matrix of 15 adult *S. ferrouensis* and may have been even more extensive on the outcrop. The shells are frequently broken and are intermixed with clams, fish scales, and numerous juveniles less than 2 mm in diameter suggesting, therefore, that they are not undisturbed spawn. Their occurrence is similar to that of other newly hatched ammonites which are found in large concentrations frequently associated with small gastropods, bivalves, foraminifers, and juvenile and adult ammonites (Wetzel, 1959; Kulicki, 1979; Birkelund, 1979; Landman, 1982a). These similarities may indicate a common benthic living association or, perhaps more likely, a mixed thanatocoenosis composed of organisms from a variety of habitats. This latter interpretation would be consistent with the hypothesis of a planktic posthatching mode of life in ammonites. Plankton are frequently preserved in otherwise benthic associations and, due to a variety of postmortem processes, may display a patchy distribution incongruent with that of the living population. On the other hand, the typical occurrence of ammonitellas in mass concentrations may imply

instead a limited dispersal capability for some time after hatching. Future finds of young postembryonic shells in environments in which benthos are excluded, e.g., anoxic black shales, may provide more substantial support for a planktic posthatching mode of life.

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LITERATURE CITED

- Bandel, K.
1982. Morphologie und Bildung der fröntonogenetischen Gehäuse bei conchiferen Mollusken. *Facies*, vol. 7, pp. 1-198.
- Bandel, K., and S. V. Boletzky
1979. A comparative study of the structure, development and morphological relationships of chambered cephalopod shells. *The Veliger*, vol. 21, pp. 318-354.
- Bandel, K., N. H. Landman, and K. M. Waage
1982. Micro-ornament on early whorls of Mesozoic ammonites; implications for early ontogeny. *Jour. Paleont.*, vol. 56, pp. 386-391.
- Birkelund, T.
1979. The last Maastrichtian ammonites. In Birkelund, T., and R. G. Bromley (eds.), *Cretaceous-Tertiary boundary events symposium 1. The Maastrichtian and Danian of Denmark*. Univ. Copenhagen, pp. 51-57.
- Birkelund, T., and J. Hansen
1974. Shell ultrastructures of some Maastrichtian Ammonoidea and Coleoidea and their taxonomic implications. *Kong. Danske. Videnskab. Sel. Biol. Skr.*, vol. 20, pp. 2-34.
- Blind, W.
1979. The early ontogenetic development of ammonoids by investigation of shell structures. *Symp. on Ammonoidea*, Syst. Assoc. York, Abstracts, p. 32.
- Boletzky, S. V.
1974. The "larvae" of Cephalopoda: a review. *Thalassia Jugoslavica*, vol. 10, pp. 45-76.

1977. Post-hatching behavior and mode of life in cephalopods. Zoological Society of London Symposium, no. 38, pp. 557–567.
- Dreyfuss, M.
1933. Découverte de nodules phosphatés à jeunes ammonites dans le Toarcien de Créveney (Haute-Saône). C.R. Somm. Soc. Géol. France, no. 14, pp. 224–226.
- Drushits, V. V., and N. Khiami
1970. Structure of the septa, protoconch walls and initial whorls in early Cretaceous ammonites. Paleont. Jour., vol. 4, pp. 26–38.
- Drushits, V. V., L. A. Doguzhayeva, and I. A. Mikhaylova
1977. The structure of the ammonitella and the direct development of ammonites. Paleont. Jour., vol. 11, pp. 188–199.
- Erben, H. K., G. Flajs, and A. Siehl
1969. Die frühontogenetische Entwicklung der Schalenstruktur ectocochleater Cephalopoden. Palaeontographica, vol. 132, pp. 1–54.
- House, M. R.
1965. A study in the Tornoceratidae: the succession of *Tornoceras* and related genera in the North American Devonian. Philos. Trans. R. Soc. London, Ser. B, vol. 250, pp. 79–130.
- Kulicki, C.
1974. Remarks on the embryogeny and post-embryonal development of ammonites. Acta. Paleontol. Pol., vol. 19, pp. 201–224.
1979. The ammonite shell: its structure, development and biological significance. *Ibid.*, vol. 39, pp. 97–142.
- Landman, N. H.
1982a. Embryonic shells of *Baculites*. Jour. Paleont., vol. 56, pp. 1235–1241.
1982b. Ontogeny and evolution of Late Cretaceous (Turonian–Santonian) Scaaphites. Unpublished Ph.D. dissertation. Yale Univ., New Haven, Connecticut, 341 pp.
- Landman, N. H., and K. M. Waage
1982. Terminology of structures in embryonic shells of Mesozoic ammonites. Jour. Paleont., vol. 56, pp. 1293–1295.
- Ockelmann, K. W.
1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. In Cox, L. R., and J. F. Peake (eds.), Proceedings of the First Malacological Congress, London, 1962. Conchological Society of Great Britain and Ireland and the Malacological Society of London, London, pp. 25–35.
- Smith, J. P.
1901. The larval coil of *Baculites*. Am. Nat., vol. 35, pp. 39–49.
- Spight, T. M.
1976. Ecology of hatching size for marine snails. Oecologia, vol. 24, pp. 283–294.
- Tanabe, K., I. Obata, Y. Fukuda, and M. Futakami
1979. Early shell growth in some Upper Cretaceous ammonites and its implications to major taxonomy. Bull. Natl. Sci. Mus., Ser. C (Geol.), vol. 5, pp. 153–176.
- Tanabe, K., Y. Fukuda, and I. Obata
1980. Ontogenetic development and functional morphology in the early growth-stages of three Cretaceous ammonites. Bull. Natl. Sci. Mus., Ser. C (Geol.), vol. 6, pp. 9–26.
- Trueman, A. E.
1940. The ammonite body chamber with special reference to the buoyancy and mode of life of the living ammonite. Quart. Jour. Geol. Soc. London, vol. 96, pp. 339–383.
- Wetzel, W.
1959. Über Ammoniten-Larven. Neues Jb. Geol. u. Paläont., Abh., vol. 107, pp. 240–252.
- Zakharov, Y. D.
1972. Formation of the caecum and prosi-phon in ammonoids. Paleont. Jour., vol. 6, pp. 201–206.